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SEED TREE RETENTION CONSIDERATIONS FOR UNEVEN-AGED MANAGEMENT IN BOLIVIAN TROPICAL FORESTS

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FREDERICKSEN, T. S., MOSTACEDO, B., JUSTINIANO, J. & LEDEZMA, J. 2001. Seed tree retention considerations for uneven-aged management in Bolivian tropical forests. Current best forestry management practices in Bolivia require the retention of seed trees after logging to provide for forest regeneration. However, current seed tree retention guidelines do not consider differences in the relative abundance of tree species, nor species-specific differences in seed production, germination, mode of regeneration, or microsite requirements that will likely affect the amount of successful regeneration produced per seed tree. In this study, we examined the ecological characteristics of timber tree species in a tropical dry forest and a tropical humid forest in Bolivia in order to classify species into groups according to the relative quantity of seed trees to be retained. Seed tree groups ranged from species that regenerate mostly from sprouts and require few (if any) seed trees, to rare tree species that reproduce primarily by seed, but with poor seed production, germination, and seedling survival that will likely require the retention of many seed trees to maintain current densities. Best management practices should consider these species differences when formulating guidelines for seed tree retention.

Key words: Bolivia - forest regeneration - seed tree - sustainable logging - tropical forests

FREDERICKSEN, T. S., MOSTACEDO, B., JUSTINIANO, J. & LEDEZMA, J. 2001. Pertimbangan pengekalan pokok biji benih dalam pengurusan umur tak seragam di hutan tropika Bolivia. Amalan semasa yang terbaik bagi pengurusan hutan di Bolivia memerlukan pengekalan pokok biji benih selepas pembalakan untuk tujuan pemulihan hutan. Bagaimanapun, panduan pengekalan pokok biji benih yang terdapat sekarang tidak mengambil kira perbezaan dalam kelimpahan relatif spesies pokok, mahupun perbezaan berdasarkan spesies dalam pengeluaran biji benih, percambahan, cara pemulihan, atau keperluan mikrosit yang mungkin mempengaruhi jumlah pemulihan yang berjaya dihasilkan bagi setiap pokok biji benih. Dalam kajian ini, kami memeriksa ciri-ciri ekologi spesies pokok balak di hutan kering tropika dan hutan lembap tropika di Bolivia bagi mengelaskan spesies kepada kumpulan tertentu berdasarkan jumlah relatif pokok biji benih yang perlu dikekalkan. Kumpulan pokok biji benih berjulat daripada spesies yang dipulihkan khususnya daripada pucuk dan memerlukan sedikit (jika ada) pokok biji benih, hinggalah kepada spesies pokok yang jarang ditemui yang membiak terutamanya daripada biji benih, tetapi akibat masalah pengeluaran biji benih yang lemah, percambahan dan kemandirian anak benih, ia mungkin memerlukan pengekalan banyak pokok biji benih untuk mengekalkan kepadatan semasa. Amalan pengurusan terbaik mestilah mengambil kira perbezaan spesies ini apabila merumuskan panduan bagi pengekalan pokok biji benih.

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Introduction

Retention of seed trees after forest harvesting is important for securing natural regeneration and ensuring the future availability of commercial timber species in tropical forests under uneven-aged management (Janzen & Vásquez-Yanes 1990, Putz 1993, Plumptre 1995). The "seed tree" method of natural reproduction is part of a recognised silvicultural system that is mostly applicable to even-aged management (Smith *et al.* 1997). In even-aged systems, a few large individuals are left per hectare to provide seed for natural regeneration after intensive cutting. Once advanced regeneration is established, these seed trees are then felled to provide more growing space for the new seedlings. Guidelines for seed tree retention in these forests are often straightforward. However, in species-rich tropical forests, selective logging guidelines for tree retention under uneven-aged management will likely be complicated because of variation among species in mature tree abundance, seed production, seed dispersal and post-dispersal survival of seeds and seedlings (Martini *et al.* 1994, Pinard *et al.* 1999).

In the tropical forests of Bolivia, the current best management practice for seed tree retention for uneven-aged management is to reserve 20% of each cutting unit from harvest as a guarantee for seed tree retention (MDSP 1998). However, these reserves do not account for species-specific differences in seed production, dispersal ability and seedling survival. For example, some tree species produce good seed crops annually, while other species may go for years without producing any seed (Justiniano & Fredericksen 2000a, b). Seed predation, germination and seedling survival also vary dramatically for important timber tree species in Bolivia (Mostacedo & Fredericksen 1999). The current general guidelines for seed tree retention in Bolivia may thus be too stringent for the regeneration requirements of some species while inadequate for the regeneration of others. In this study, we examined the ecological characteristics of tree species in a tropical dry forest and a tropical humid forest in Bolivia in order to classify species groups according to the relative quantities of seed trees to be retained after selective harvesting in these forests.

Materials and methods

Study sites

Las Trancas is a seasonally dry tropical forest owned and managed by the Chiquitano indigenous community within the Lomerío region south of Concepción (16° 13' S, 61° 50' W) in eastern Bolivia. Seasonal mean temperature in the region averages about 24.3 °C with a mean annual precipitation of about 1100 mm. Most of Las Trancas is upland forest with the 14–18 m open-canopy stratum becoming mostly deciduous during a six month dry season. The upland portions of the site include approximately 50 canopy tree species, most numerous of which are *Anadenanthera colubrina* and *Acosmium cardenasii.* Light selective logging for Spanish cedar (*Cedrela fissilis*), Spanish oak (*Amburana cearensis*), and morado (*Machaerium scleroxylon*) has been carried out at undetermined intervals on the site. Currently, 11 species are harvested commercially in Las Trancas, but 10 other species have timber quality that may permit commercial harvesting in the future and were thus included in the analyses of this study.

La Chonta Ltda. is a timber concession located within the Guarayos Forest Reserve in eastern Bolivia (15° 45' S, 62° 60' W). The site is classified as a humid tropical forest with a mean annual temperature of 24.5 °C and mean annual rainfall of approximately 1500 mm. Some species become deciduous during a three-month dry season, but most trees remain evergreen. The closed forest canopy averages 20–22 m tall and is dominated by tree species characteristic of moist forests in Bolivia, including *Hura crepitans, Ficus glabrata,* and *Pseudolmedia laevis.* Fifteen species are being managed for timber production in this concession.

Forest inventory

Pre-harvest forest inventories were carried out in Las Trancas in 1994 and La Chonta in 1996. These results were used to classify tree species to seed tree groups based on their relative abundance and distribution within the forests. The diameter and abundance of all commercial tree species > 20 cm dbh were recorded. In Las Trancas, this inventory was conducted using 100 permanent plots measuring 50 × 50 m distributed in a stratified random fashion throughout the 100-ha management area. In La Chonta, forest inventory was conducted throughout 100 ha of forest to be harvested in 1997.

Tree species phenology and fruit production

Phenological data on commercial tree species in Las Trancas were derived from phenological studies conducted by Justiniano and Fredericksen (2000a, b). In that study, 10 trees of each species (and other non-commercial species not recorded here) were selected for monthly observations of seed production from 1995 till 1997. In La Chonta, formal phenological studies of tree species were only recently initiated by the authors in May 1999 using similar methodology to that used in Las Trancas. However, phenological observations during research carried out over the previous two years as part of a study of fig tree regeneration (Fredericksen *et al.* 1999) were used to determine the fruit production phenology of commercial tree species. Observations of seedling germination and seed predation were noted during the phenological studies.

Seedling regeneration success

In Las Trancas, seedling and sprouting regeneration of commercial species were recorded during the first-year following logging in 36 plots (1 × 1 m) replicated in each of the following locations: log landings, principal logging roads, log extraction paths, logging gaps, and in areas undisturbed by logging. This work was part of a larger study on the regeneration of plant communities following logging. In La Chonta, commercial species regeneration was observed in 10 transects of size 50 × 4 m conducted in each of these three areas: forests burned two years previously by wildfire, forest selectively logged one year previously, and undisturbed forest. This work was part of a larger study of fig tree regeneration (Fredericksen *et al.* 1999). Based on these data, the microhabitat preferences for regeneration of each species at each study site were determined.

Designation of seed tree groups

Species for each study site were assigned into seed tree retention groups. The classification was based on the relative pre-harvest abundance of trees, the relative abundance of seeds, frequency of seed crops and germination success. Classification also depended on whether the survival of species was dependent on disturbances that control competing vegetation (soil disturbance, gap formation or fire), whether the species depended mostly on seed or sprouting for regeneration, or whether their seeds were animal- or wind-dispersed. The breeding systems (monoecious, dioecious, hermaphrodite) of tree species were also considered. Species that are dioecious were noted because the male individuals of these species are not capable of producing seed.

The following definitions were used for assigning tree species into seed tree groups: common species were defined as having a density of > 2 trees ha^{-1}, trees with regular seed production were defined as producing abundant seed crops (> 500 seeds $tree^{-1}$) at least every other year, and high germination success was defined as having > 50% germination capacity and < 50% seed predation rate. Most assignments for species were based on quantitative data collected by the authors, although some assignments were estimates based on field knowledge of the species.

Results and discussion

Based on characteristics of timber species related to seed tree retention, it was apparent that tree species at Las Trancas and La Chonta differ in abundance, method of reproduction, seed production, dispersal, and seedling survival (Tables 1 & 2). These differences appeared to be sufficient to warrant species-specific or species group-specific guidelines for seed tree retention. Based on similarities in these characteristics, a dichotomous key was developed for each study site to preliminarily assign species to seed tree retention groups (Tables 3 & 4).

The first obvious separation for seed tree retention appeared to be for those species that reproduce almost exclusively by sprouting from cut stumps and damaged roots as opposed to species that regenerate predominantly from seed. Regeneration of sprouting species (Group I) was encountered in abundance on the borders of logging roads or in logging gaps. Damage to roots of mature trees bordering roads formed due to the passage of logging trucks and skidders, appeared to have stimulated this sprouting. Sprouts also occurred from the bases of harvested stems and other smaller stems damaged during road construction or logging. For these species, it was rare to find seed-origin regeneration in any location within the forest due to one or more factors such as low seed viability, poor germination capacity, high rate of seed predation and poor seedling survival. The most extreme example of this group was *Centrolobium microchaete.* Examination of seeds of this species indicated that only 10% of seeds were sound and capable of germination. However, only 4% of these seeds actually germinated (Justiniano & Fredericksen 1998b). Finally, high rates of pre-dispersal seed predation by parrots and squirrels as well as high rates of post-dispersal seed predation by insects, were observed. Therefore, for these sprouting species, seed tree retention is largely unnecessary for regeneration and guidelines may exclude these species. However, it may be desirable to retain large trees of these species for other purposes such as regulation of wood flow over cutting cycles, maintenance of

Table 1. Characteristics of timber tree species related to seed tree retention in the tropical dry forest of Las Trancas, Lomerío in eastern Bolivia

Species	Adult density[1] (trees ha^{-1})	Seed interval[2] (year)	M/D[3]	Seed pro-duction[4]	Germi-nation[5]	Mode of dispersal	Microhabitat for regeneration[6]	Mode of regeneration
Amburana cearensis	0.5	> 2	M	Poor	Fair	Wind	Rocky soils	Seed
Anadenanthera colubrina	42.6	1–2	M	Good	Good	Gravity	Disturbed soils	Seed
Aspidosperma cylindrocarpon	5.1	1–2	M	Fair	Good	Wind	Forest floor	Seed
Aspidosperma rigidum	9.5	1–2	M	Good	Good	Wind	Forest floor	Seed
Astronium urundeuva	4.2	1	D	Good	Good	Wind	Disturbed soils	Seed
Caesalpinia pluviosa	4.0	1	M	Good	Good	Gravity	Disturbed	Seed and sprout
Calycophyllum multiflorum	0.2	1	M	Good	Fair	Wind	Forest floor	Seed
Cariniana ianeirensis	1.5	> 2	M	Good	Good	Wind	Forest floor	Seed
Cedrela fissilis	0.1	> 2	M	Good	Fair	Wind	Rocky soils	Seed
Centrolobium Microchaete	7.9	1	M	Poor	Poor	Wind	Disturbed soils	Sprout
Copaifera chodatiana	4.6	1	M	Good	Good	Animal	Forest Floor	Seed
Cordia alliodora	0.1	1	M	Good	Fair	Wind	Distrubed soils	Seed
Hymenaea courbaril	1.0	> 2	M	Fair	Fair	Animal	Forest floor	Seed
Machaerium scleroxylon	5.5	> 2	M	Good	Poor	Wind	Disturbed soils	Seed
Phyllostylon rhamnoides	4.2	1–2	M	Good	Fair	Wind	Forest floor	Seed
Platymiscium ulei	1.1	> 2	M	Good	Poor	Wind	Disturbed soils	Sprout
Platypodium elegans	1.4	> 2	M	Good	Poor	Wind	Clearings	Seed
Schinopsis brasiliensis	1.2	1	M	Good	Poor	Wind	Distrubed soils	Seed
Spondias mombin	1.4	1	M	Good	Fair	Animal	Disturbed soils	Sprout
Tabebuia impetiginosa	6.9	1–2	M	Good	Poor	Wind	Disturbed soils	Sprout
Tabebuia serratifolia	0.2	1–2	M	Good	Poor	Wind	Forest floor	Seed

1. Density of trees > 20 cm dbh per hectare
2. Number of years between seed crops
3. Monoecious (M) or dioecious (D) habit
4. Seed production: Good – produces > 1000 sound seeds per tree; Fair – produces between 200–1000 sound seeds per tree; Poor – produces < 200 sound seeds per tree
5. Germination capacity and freedom from seed predation: Good – germination capacity is > 50% and seed predation is < 15%; Fair – germination capacity is < 50% or seed predation is > 50%; Poor – germination capacity is < 50% and seed predation is > 50%
6. Locations within the forest where most regeneration of species occurs

Table 2. Characteristics of timber tree species related to seed tree retention in the tropical humid forest of La Chonta in eastern Bolivia

Species	Adult density[1] (trees ha^{-1})	Seed interval[2] (year)	M/D[3]	Seed production[4]	Germination[5]	Mode of dispersal	Microhabitat for regeneration[6]	Mode of regeneration
Ampelocera ruizii	6.7	1	M	Good	Good	Animal	Forest floor	Seed
Aspidosperma cylindrocarpon	1.5	1–2	M	Fair	Good	Wind	Forest floor	Seed
Cariniana domestica	0.5	1–2	M	Good	Fair	Wind	Forest floor	Seed
Cariniana estrellensis	0.5	1–2	M	Good	Fair	Wind	Forest floor	Seed
Cariniana ianeirensis	2.4	1–2	M	Good	Fair	Wind	Forest floor	Seed
Centrolobium microchaete	0.9	1	M	Poor	Poor	Wind	Disturbed soils	Sprout
Ficus catappifolia	0.2	1–2	M	Good	Good	Animal	Disturbed soils	Seed
Ficus glabrata	1.5	1–2	M	Good	Good	Animal	Disturbed soils	Seed
Gallesia integrifolia	3.0	1	M	Good	Good	Wind	Forest floor	Seed
Hura crepitans	3.7	1	M	Good	Good	Gravity	Widespread	Seed
Pseudolmedia laevis	11.2	1	D	Good	Good	Gravity	Forest floor	Seed
Schizolobium amazonicum	1.1	1	M	Good	Good	Wind	Distrubed soils	Seed
Spondias mombin	1.4	1	M	Good	Fair	Animal	Disturbed soils	Sprout
Swietenia macrophylla	0.4	1	M	Good	Good	Wind	Disturbed soils	Seed
Terminalia oblonga	6.5	1	M	Good	Good	Wind	Forest floor	Seed

1. Density of trees > 20 cm dbh per hectare
2. Number of years between seed crops
3. Monoecious (M) or dioecious (D) habit
4. Seed production: Good – produces > 1000 sound seeds per tree; Fair – produces between 200–1000 sound seeds per tree; Poor – produces < 200 sound seeds per tree
5. Germination capacity and freedom from seed predation: Good – germination capacity is > 50% and seed predation is < 15%; Fair – germination capacity is < 50% or seed predation is > 50%; Poor – germination capacity is < 50% and seed predation is > 50%
6. Locations within the forest where most regeneration of species occurs

Table 3. Key to seed tree species groups in the tropical dry forest of Las Trancas, Lomerío in eastern Bolivia

I. **Species that reproduce predominantly by sprouting**

Regeneration by seed extremely rare, but quite common from root sprouts on logging roads and from cut stumps. ***Species which need few, if any, seed trees retained.***

Centrolobium microchaete
Platymiscium ulei
Spondias mombin
Tabebuia impetiginosa

II. **Species that reproduce predominantly by seed**

A *Common species that frequently produce good seed crops, with high germination success*

1. Species tolerant of competing vegetation (Group IIA 1) - Advanced regeneration commonly occurs under closed canopy. ***Low numbers of seed trees required, microsite conditions not critical.***

    (a) Wind-dispersed – *Aspidosperma cylindrocarpon*
    Aspidosperma rigidum
    Phyllostylon rhamnoides

    (b) Gravity- or animal-dispersed – *Copaifera chodatiana*

2. Species intolerant of competing vegetation (Group IIA 2) - Advanced regeneration rarely observed under closed forest, but is abundant in areas with high light (logging gaps) and/or areas where soil disturbance by logging has eliminated competing vegetation. ***Low numbers of seed trees required, microsite conditions critical.***

    (a) Wind-dispersed – *Anadenanthera colubrina*
    Astronium urundeuva

    (b) Gravity-dispersed – *Caesalpinia pluviosa*

B *Rare species and/or species that infrequently produce good seed crops or have poor germination success*

Species with an abundance of < 2 trees ha^{-1} that irregularly produce good seed crops (> 500 seeds trees), have germination capacities < 50% and/or seed predation rates > 50%. ***Relatively high number of seed trees required.***

1. Species tolerant of competing vegetation (Group IIB 1) - Advanced regeneration commonly occurs under closed canopy. ***High numbers of seed trees required, microsite conditions not critical.***

    (a) Wind-dispersed – *Calycophyllum multiflorum*
    Cariniana ianeirensis

    (b) Gravity- or animal-dispersed – *Hymenaea courbaril*

2. Species intolerant of competing vegetation (Group IIB 2) - Advanced regeneration rarely observed under closed forest, but is abundant in areas with high light (logging gaps) and/or areas where soil disturbance by logging has eliminated competing vegetation. ***High numbers of seed trees required, microsite conditions critical.***

    (a) Wind-dispersed – *Amburana cearensis*
    Cedrela fissilis
    Cordia alliodora
    Machaerium scleroxylon
    Platypodium elegans
    Schinopsis brasiliensis
    Tabebuia serratifolia

    (b) Gravity- or animal-dispersed – none

Table 4. Key to seed tree species groups in the tropical humid forest of La Chonta in eastern Bolivia

I. **Species that reproduce predominantly by sprouting**

Regeneration by seed extremely rare, but quite common from root sprouts on logging roads and from cut stumps. ***Species which need few, if any, seed trees retained.***

Centrolobium microchaete
Spondias mombin

II. **Species that reproduce predominantly by seed**

A *Common species that frequently produce good seed crops and have high germination success*

Species tolerant of competing vegetation (Group IIA 1) - Advanced regeneration commonly occurs under closed canopy. ***Low numbers of seed trees required, microsite conditions not critical.***

(a) Wind-dispersed – *Cariniana ianeirensis*
Gallesia integrifolia
Terminalia oblonga

(b) Gravity- or animal-dispersed – *Pseudolmedia laevis* (dioecious)
Ampelocera ruizii
Hura crepitans

2. Species intolerant of competing vegetation (Group IIA 2) - Advanced regeneration rarely observed under closed forest, but is abundant in areas with high light (logging gaps) and/or areas where soil disturbance by logging has eliminated competing vegetation. ***Low numbers of seed trees required, microsite conditions critical.***

(a) Wind-dispersed – None

(b) Gravity-dispersed – None

B *Rare species and/or species that infrequently produce good seed crops or have poor germination success*

Species with an abundance of < 2 trees ha^{-1} that irregularly produce good seed crops (> 500 seeds $tree^{-1}$), have germination capacities < 50% and/or have > 50% seed predation rates. ***Relatively high number of seed trees required.***

1. Species tolerant of competing vegetation (Group IIB 1) - Advanced regeneration commonly occurs under closed canopy. ***High numbers of seed trees required, microsite conditions not critical.***

(a) Wind-dispersed – *Aspidosperma cylindrocarpon*
Cariniana domestica
Cariniana estrellensis

(b) Gravity- or animal-dispersed – none

2. Species intolerant of competing vegetation (Group IIB 2) - Advanced regeneration rarely observed under closed forest, but is abundant in areas with high light (logging gaps) and/or areas where soil disturbance by logging has eliminated competing vegetation. ***High numbers of seed trees required, microsite conditions critical.***

(a) Wind-dispersed – *Schizolobium amazonicum*
Swietenia macrophylla

(b) Gravity- or animal-dispersed – *Ficus catappifolia*
Ficus glabrata

gene flow in the population, and retention of trees which bear fruits important for wildlife. It is also important to determine whether sprouts will result in well-formed individuals with adequate stocking.

Another important separation for seed tree retention guidelines is mature tree abundance. The more common the tree species, the less likely it is to be made rare by selective harvesting, unless a common species is so exceptionally valuable that all mature trees are likely to be cut. However, none of the common species considered here have such high values, nor would the current minimum-diameter cutting regulations in Bolivia permit this to occur (MDSP 1998). For all tree species, especially rare ones, harvesting may create large distances between mature individuals of a species resulting in low pollination success. Forest tree seeds are usually produced by cross pollination and wind pollination is almost non-existent in tropical forests (Bawa 1990, Janzen & Vásquez-Yanes 1990). Therefore, seed tree retention guidelines should pay special attention to the tree pollination biology of individual species and to the maintenance of their animal pollinators. Unfortunately, little is known about the pollination mechanisms for most of Bolivian tropical forest tree species. Pollinators are often capable of travelling great distances in tropical forests (Nason *et al.* 1997). However, decreases in tree densities have been shown to decrease pollination success (House 1992, 1993). The pollinator isolation problem is especially acute for fig tree species, whose asynchronous fruiting habit presents challenges for the survival of wasp pollinators upon which fig tree species depend on for pollination (Ramirez 1970). However, the poor stem quality of the fig tree species at La Chonta may prevent harvesting of fig trees that results in low fig population densities (Fredericksen *et al.* 1999).

For some rare species that were restricted to certain habitats, isolation of mature trees was less of a problem. Examples included *Cariniana ianeirensis, Hymenaea courbaril* and *Tabebuia serratifolia* in Las Trancas. These species were rare, but only because they were restricted to riparian areas. Within riparian areas, these species could actually be relatively common. These areas are also protected from harvesting under Bolivian law. Therefore, designating seed tree retention guidelines for these species may be related to current protection laws at this study site. In general, however, seed tree retention guidelines should be much more stringent for rare species (Group IIB) than common species (Group IIA), especially those with wider distributions and high commercial value. Species such as *Amburana cearensis, Cedrela fissilis* and *Swietenia macrophylla* are all relatively rare upland tree species that have been over-harvested in the past. Seed tree guidelines should be more stringent to protect these species from becoming commercially extinct. In some cases, the current abundance of these species may already be below densities necessary to provide regeneration sufficient to replace harvested trees. In these cases, enrichment planting may be necessary to restore the abundance of these species to a level where natural regeneration may again proceed.

Similar to trees with high mature tree abundance, species with frequent and abundant seed production should not require seed tree retention guidelines as restrictive as those species which produce poor seed crops or only infrequently produce good seed crops. For example, in Las Trancas, *Copaifera chodatiana* produced good seed crops nearly every year and each seed tree had the opportunity to regenerate annually. Conversely, *Platypodium elegans* had poor seed production and intervals with no seed production which could last several years. For species such as this, a higher number of seed trees should be retained to ensure a higher probability of regeneration success during years of good seed tree production. It is also important to consider species differences in the relationship between tree size and seed production. Generally, larger trees will produce more seeds up to the point of senescence (Smith *et al.* 1997). Therefore, diameter-limit harvesting will tend to eliminate the best seed trees unless specific provisions are made for the retention of larger trees (Plumptre 1995). However, the amount of seed produced may vary with the increasing size of tree species. In Bolivia, diameter-limit cutting is mandated under the current forestry law, without an understanding of its impacts on seed production of timber species. Studies are needed to quantify the relationship between seed production and tree size in Bolivian tree species.

A further dichotomy for seed-tree retention guidelines that should be recognised is the likelihood for germination and survival of seeds from trees retained after harvesting. This survival will be largely dependent upon the regeneration microsites required by each species. Leaving seed trees may be of little use if post-logging conditions do not favour the subsequent establishment and survival of seedlings. For example, light-seeded, shade-intolerant species, such as *Astronium urundeuva* and *Cedrela fissilis* may not regenerate well in forests receiving light and also selective logging, regardless of the number of seed trees retained. If sustainable harvesting of these species is an objective, it may be more appropriate to harvest forest stands more intensively leaving fewer seed trees, but provide conditions suitable for the regeneration success of these species (Fredericksen 1998). The number of seed trees retained should therefore also be based on the likely regeneration success of these species under the post-harvest site conditions.

Type of seed dispersal mechanism is another factor to consider for seed tree retention. For example, for 34 wind-dispersed tree species on Barro Colorado Island in Panama, Augspurger (1986) found that the mass and area of seeds varied over six orders of magnitude leading to dispersal distances varying from 22–194 m. However, Smith *et al.* (1997) noted that animals and wind can usually provide good seed dispersal. This suggests that the quantity of seed and the nature of microsites may be more important for determining seed tree retention. This observation is most likely to be true for the tree species in both forests of this study. Strong dry season winds promote the long-range dispersal of anemochorus species, while animal species are known to be good long-range dispersers for most non-anemochorus species (Justiniano & Fredericksen 2000b). For example, even though the more fleshy-seeded species in the Las Trancas forest do not possess hard exocarps (*Caesalpinia pluviosa, Copaifera chodatiana* and *Adadenanthera colubrina*) and are unlikely to survive passing through the digestive tracts of animals, they appear to be dispersed to significant distances away from parent trees by leaf-cutter ants (*Atta* spp.) (Fredericksen & Justiniano 1998, Justiniano & Fredericksen 1998a, b). While leaf-cutter ants cause mortality of many seeds transported to underground colonies, many are abandoned along ant trails. While dispersal mechanism may appear less important for tropical tree species, seed dispersal patterns are complex, and implications for their management are not well understood (Janzen & Vásquez-Yanes 1990). Although none of the tree species in the forests of this study appeared to have restricted dispersal, it may be important to distinguish species by dispersal method in other forests, where dispersal restrictions might occur.

A final consideration for seed tree retention is that dioecious trees will typically have half the dispersal ability of monoecious species. Therefore, species such as *Astronium urundeuva* in Las Trancas and *Pseudolmedia laevis* in La Chonta will likely require twice the number of seed trees to obtain similar regeneration relative to a monoecious species with an otherwise similar regeneration ecology. In addition, many hermaphrodite or female trees never set seed. Therefore, it is often not possible to predict which trees will be good seed producers. The observation of seeds on a tree may be the only certain method of determining which trees should be retained after harvesting as seed trees (Smith *et al.* 1997).

The selection of trees as seed trees in tropical forests is more complicated than simply leaving large trees (Smith *et al.* 1997), or in the case of Bolivia, leaving seed tree reserves. Species-specific differences in seed and seedling ecology should be considered so that seed trees are not left unnecessarily with subsequent negative economic implications, nor in insufficient numbers that would hinder post-harvest regeneration. In most cases, seed tree retention remains a subjective endeavour. More detailed information on the regeneration ecology of tropical species is needed to permit more precise, quantitative guidelines for seed tree retention. However, the construction of a dichotomous key based on individual species characteristics, such as the ones presented in this study, may help forest managers plan more effectively for the retention of seed trees in harvested forests. The classification presented here should not be applied to other forests without review of its local usefulness. The structure and specifications of the classification will likely need to be modified based on the availability of data on local tree species, forest conditions and management strategies.

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